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Cytonuclear Introgressive Swamping and Species Turnover of Bass After an Introduction

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Species-specific RFLP markers from mitochondrial DNA (mtDNA) were identified and employed in conjunction with previously reported data for nuclear allozyme markers to examine the genetic consequences of an artificial introduction of spotted bass (*Micropterus punctulatus*) into a north Georgia reservoir originally occupied by native smallmouth bass (*M. dolomieui*). The cytonuclear genetic data indicate that within 10–15 years following the unauthorized introduction, a reversal in these species' abundances has occurred and that more than 99% of the population sample analyzed here consists of spotted bass or products of interspecific hybridization. This demographic shift, perhaps ecologically or environmentally mediated, has been accompanied by introgressive swamping; more than 95% of the remaining smallmouth bass nuclear and cytoplasmic alleles are present in individuals of hybrid ancestry. Dilocus cytonuclear disequilibria were significantly different from zero, with patterns indicative of an excess of homospecific genetic combinations (relative to expectations from single-locus allelic frequencies) and a disproportionate contribution of smallmouth bass mothers to the hybrid gene pool. Results document dramatic genetic and demographic changes following the human-mediated introduction of a nonnative species.

This article is a followup to a previous report by Pierce (1995) that evaluated hybridization between black basses (Centrarchidae; *Micropterus*) in several reservoirs of the southeastern United States following artificial introductions outside the species' native ranges. Special attention is focused here on a *Micropterus* population in a northeast Georgia reservoir, Lake Chatuge, where allozyme assays by Pierce (1995) confirmed suspicions from morphological evidence that extensive introgressive hybridization has taken place between introduced spotted bass (*M. punctulatus*) and native smallmouth bass (*M. dolomieui*). Lake Chatuge is a man-made reservoir in the upper reaches of the Tennessee River drainage, within the historical range of *M. dolomieui.* Initially, Lake Chatuge supported an active sport fishery for smallmouth bass, but unauthorized introductions of unknown numbers of *M. punctulatus* in the late 1970s initiated a faunal changeover involving a dramatic decline in smallmouth abundance and replacement by spotted bass and probable hybrids. The spotted bass that were introduced (most likely by members of a bass-fishing club) are thought to have been taken from Lake Lanier, in the Chattahoochee River drainage of north-central Georgia (Weaver R, Georgia Department of Natural Resources, personal communication).

Here we add mitochondrial DNA (mtDNA) to the genetic analysis of the Lake Chatuge population by identifying and screening species-diagnostic markers for this maternally transmitted molecule. In conjunction with the nuclear markers previously identified by Pierce (1995), this cytoplasmic information was obtained to yield further insights into the magnitudes and patterns of introgression, including the possibility of gender-based asymmetries in the hybridization process. Although other genetically confirmed reports of introgressive hybridization between black basses exist (Koppelman 1994; Morizot et al. 1991; Philipp et al. 1983; Whitmore 1983; Whitmore and Butler 1982; Whitmore and Hellier 1988), none has explored the unique perspectives that a cytonuclear genetic analysis can provide.

Materials and Methods

Collections

To identify potential species-diagnostic mtDNA markers, spotted bass were as-

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sayed from Lake Lanier, Georgia, in the Chattahoochee River basin (N = 9), and from Carters Lake, Georgia, in the Alabama River basin (N = 15). At both locales, the Alabama subspecies of spotted bass is native and no smallmouth bass have been reported (Pierce 1995; Robbins and MacCrimmon 1974). Lake Lanier is also the presumed source of the introduction of spotted bass into Lake Chatuge. Smallmouth bass were assayed from Dale Hollow Reservoir, Tennessee, in the Tennessee River basin (N = 10). Although both smallmouth and the northern spotted bass are native to this locale, the individuals sampled to identify smallmouth mtDNA markers appeared to be genetically "pure," as gauged both from morphological appearance and by fixed allozyme differences from spotted bass as assessed in a larger collection of fish (N = 52) from that reservoir (Pierce 1995).

Largemouth bass (*M. salmoides*) also occur in Lake Chatuge. Thus, for the sake of completeness, potential mtDNA markers for this species were identified from a reference sample taken from Lake Oconee, Georgia, in the Altamaha River basin (N = 18). As judged by restriction fragment length polymorphism (RFLP) digests of these samples, largemouth bass mtDNA is readily distinguishable from that of both smallmouth and spotted bass. However, no mtDNA genotypes characteristic of largemouth bass were uncovered in the smallmouth/spotted bass collections from the Lake Chatuge collection considered in this report, so this species will not be treated further here.

On October 20, 1994, 251 fish displaying phenotypes of the spotted/smallmouth/hybrid complex were sampled from Lake Chatuge, of which 246 individuals subsequently were assayed successfully for mtDNA (and allozyme) markers. Fish were collected by electroshocking from several boats patrolling scattered shoreline locations around the lake, with no particular effort to "target" particular *Micropterus* species. Thus, barring possible inadvertent sampling biases (e.g., via habitat or depth), the pooled collection can be considered a random sample of spotted and smallmouth bass and their hybrids.

Laboratory Assays

Mitochondrial DNA was isolated in closed-circular form from liver and heart tissues via CsCl density gradient purification as described by Lansman et al. (1981). Purified mtDNA was digested with restriction enzymes (following manufacturers' recommendations), radioactively end-labeled with ^{35}S nucleotides, and electrophoresed through 1.0–1.6% agarose gels. Development of autoradiographs revealed digestion profiles for 11 restriction enzymes in the initial population screenings (*Ava*II, *Bcl*I, *Bgl*II, *Dra*II, *Hin*cII, *Hin*dIII, *Kpn*I, *Ksp*I, *Nde*I, *Pvu*II, and *Spe*I). Digestion patterns for most of the enzymes were species diagnostic in these samples, and four of the most readily scored systems (*Ava*II, *Dra*II, *Hin*cII, and *Spe*I) were subsequently assayed as markers of maternal ancestry for 186 individuals from Lake Chatuge.

Another 60 of the Lake Chatuge specimens were too small to recover sufficient amounts of intact circular mtDNA for standard RFLP analyses, so other methods had to be employed. A 2.0 kb fragment containing the control region and adjacent areas from CsCl-purified mtDNA was amplified from nine bass outside Lake Chatuge (three from each of the three *Micropterus* species) using the primers Pro-L and 12 Sar-H (Palumbi et al. 1991), and *Taq* polymerase (Promega). From each sample, 10 μl of amplified DNA was digested without further purification and visualized using EtBr in agarose gels. Thirty-two restriction enzymes were used to screen for polymorphisms, and three of these (*Dra*I, *Hin*cII, and *Msp*I) revealed potential species-specific digestion profiles. This specificity was confirmed by using the same in vitro assay procedure on the same 2.0 kb fragment in 20 additional individuals from each of the bass species, and by digesting with the three enzymes mentioned above. Then, to determine the species of origin for the mtDNA of the 60 smaller fish from Lake Chatuge, total DNA was isolated from each specimen using a phenol-chloroform method described in Karl et al. (1992), followed by amplification and digestion with the three diagnostic restriction enzymes.

Statistical Analyses

Data were summarized using the cytonuclear disequilibrium statistics introduced by Asmussen et al. (1987). Briefly, the gametic or allelic disequilibrium, D, measures associations between the two alleles at a diploid nuclear gene (e.g., an allozyme locus) and a uniparentally transmitted, haploid cytoplasmic gene (e.g., mtDNA); and three genotypic disequilibria, D_1, D_2, and D_3, measure associations between the two cytotypes and the three respective nuclear genotypic classes (the two homozygotes and the heterozygote). Anticipated properties of these population-level statistics under various mating system and gene flow models in hybrid zones have been considered in a series of theoretical treatments (review in Arnold 1993; Arnold et al. 1988; Asmussen and Arnold 1991; Asmussen et al. 1989).

Results

As judged by mtDNA digestion profiles in the reference spotted and smallmouth bass samples taken outside Lake Chatuge, the two species can be readily distinguished with these cytoplasmic markers (notwithstanding evident within-species variation; Figure 1). Among the 11 endonucleases employed in the initial screens, all except *Hin*dIII showed diagnostic species differences, often involving more than a single restriction site change (although no attempt was made to formally map restriction sites or to further characterize the mtDNA differences).

Digestion profiles for the four species-diagnostic restriction enzymes employed to assay the majority of the bass samples from Lake Chatuge are shown in Figure 1. These patterns were invariably consistent in diagnosis of species origin—for example, if the profile in the *Ava*II digest indicated spotted bass mtDNA origin for an individual, so too did the digestion profiles for the other three endonucleases. Furthermore, profiles for each of the four enzymes differed between spotted and smallmouth bass by multiple restriction site changes. Thus, the possibility of misclassification of species origin for an mtDNA genotype in the Lake Chatuge bass was negligible.

Single-locus Nuclear by Mitochondrial Associations

Numerous fish displaying cytonuclear genotypes other than those expected in pure spotted bass or smallmouth bass were present in the Lake Chatuge collection (Table 1). Nonetheless, allelic and genotypic disequilibria were highly significantly different from zero in all cases, indicating strong nonrandom cytonuclear associations (Table 2). These associations are in the direction of an excess of homospecific cytonuclear combinations relative to random-assortment expectations (positive values for D and D_1, and negative values for D_3), and a disproportionately high representation of smallmouth bass mtDNA in the heterozygous class of genotypes at each nuclear locus (negative values for D_2).

The magnitudes and patterns of cytonuclear association are remarkably consis-

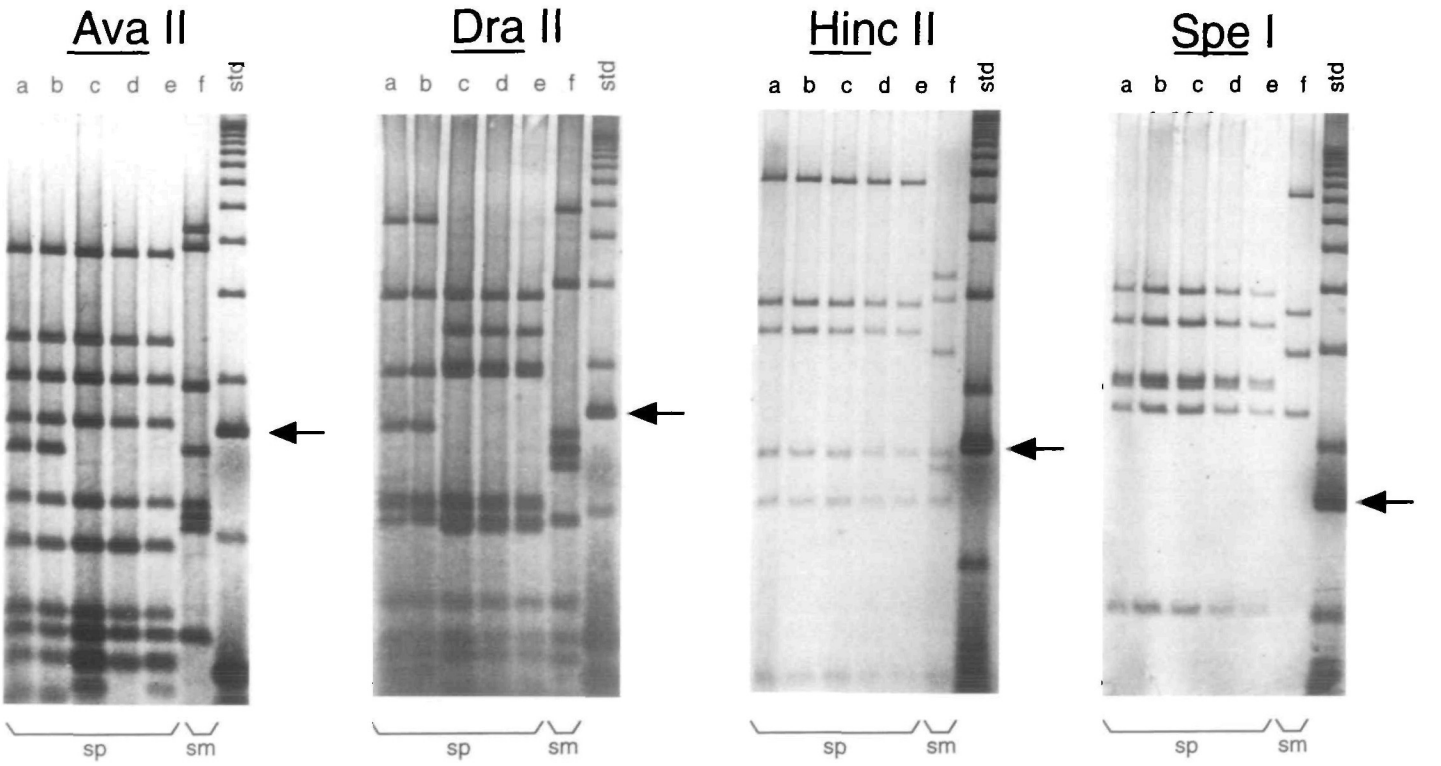

Figure 1. mtDNA digestion profiles of four species-diagnostic restriction enzymes (in our collections) employed to survey the majority of individuals from Lake Chatuge. In each gel, lanes a–e are spotted bass profiles, lane f is the smallmouth bass profile, and the rightmost lane is a 1 kb molecular weight standard (the arrows point to the 1.6 kb band). Note from the *Ava*II and *Dra*II digests (compare lanes a and b against c–e) that considerable intraspecific mtDNA polymorphism was present among spotted bass, as was also true for smallmouth bass for some of the enzymes employed (not shown).

Table 1. Cytonuclear genotypic counts for the 246 specimens of black bass sampled from Lake Chatuge

mtDNA	AA	AB	BB	Total
Malate dehydrogenase-B (*sMDH-B*)				
M	198	25	1	224
	(183.0)	(36.4)	(4.6)	
m	3	15	4	22
	(18.0)	(3.6)	(0.5)	
Total	201	40	5	246
Phosphoglucomutase-A (*PGM-A*)				
M	209	15	0	224
	(194.8)	(25.5)	(3.6)	
m	5	13	4	22
	(19.1)	(2.5)	(0.4)	
Total	214	28	4	246
Esterase-2 (*EST-2*)				
M	208	13	3	224
	(194.0)	(22.8)	(7.3)	
m	5	12	5	22
	(19.0)	(2.2)	(0.7)	
Total	213	25	8	246

At each nuclear locus, A and B refer to marker alleles from spotted bass and smallmouth bass, respectively. For mtDNA, the respective haplotypes from these two species are denoted M and m. In parentheses are expected counts for the cytonuclear genotypes calculated from the marginal frequencies, assuming random associations.

tent across all three nuclear loci (Table 2). This strongly suggests that the processes responsible were genomically pervasive, rather than idiosyncratic to particular genes, and eliminates potential locus-specific effects such as strong selection directed at particular alleles. In principle, candidates for such genomically pervasive forces include population admixture with positive assortative (homospecific) mating, continued recruitment of pure parental species into the hybrid population, and selection against hybridity per se.

By procedures described in the next section, genetically pure spotted and smallmouth bass individuals can provisionally be distinguished from hybrids through examination of multilocus marker genotypes. Removal of such individuals from Table 1 reveals the cytonuclear patterns within the class of fishes of presumed hybrid ancestry (Table 3). This culling procedure severely reduced sample sizes and thereby diminished the power of the statistical tests, but nonetheless, several of the cytonuclear disequilibria in hybrids remained significant, and the directions of the departures from random-association expectations were identical to those registered in the total data set of Table 1. Thus the tendencies were for excesses of homospecific cytonuclear combinations in hybrids, and for a disproportionate representation of smallmouth bass mtDNA among the heterozygotes at nuclear loci.

Multilocus Cytonuclear Associations

In our approach, an individual was provisionally considered to be a pure spotted or smallmouth bass if homozygous for the appropriate alleles at all three nuclear marker loci, an F_1 hybrid if heterozygous at all marker genes, a backcross (generation unspecified) to one or the other parental species if homozygous for the appropriate alleles at one or more loci and heterozygous at others, and a later-generation nonbackcross hybrid if alternately homozygous at these marker loci for alleles from the two parental species. Two caveats should be mentioned. First, the allozyme markers are not strictly fixed for alternate alleles in the two species, but only nearly so (Pierce 1995). However, this difficulty is unlikely to be important in the current study because among the sampled reference populations the highest (and only) frequency of a "wrong" allele in a "pure" species sample was 0.014 (for the

Table 2. Application of cytonuclear disequilibrium statistics to the allozyme by mtDNA data presented in Tables 1 and 3 for the Lake Chatuge collections of black bass[a]

Category	D	D_1	D_2	D_3
Total collection (N = 246)				
sMDH-B				
Estimate	**0.037**	**0.061**	**−0.046**	**−0.014**
Normalized[b]	0.822	0.833	−0.620	−0.780
Standard error	0.008	0.013	0.012	0.007
PGM-A				
Estimate	**0.036**	**0.057**	**−0.043**	**−0.015**
Normalized[b]	0.780	0 739	−0.538	−1.000
Standard error	0.009	0.013	0.012	0.007
EST-2				
Estimate	**0.037**	**0.057**	**−0.040**	**−0.017**
Normalized[b]	0.696	0.738	−0.494	−0.588
Standard error	0.009	0.013	0.011	0.008
Individuals of hybrid genotype (N = 67)				
sMDH-B				
Estimate	0.044	0.063	−0.037	−0.026
Normalized[b]	0.598	0.584	−0.291	−0.636
Standard error	0.016	0.024	0.027	0.017
PGM-A				
Estimate	**0.062**	**0.094**	−0.063	−0.031
Normalized[b]	0.625	0.557	−0.346	−1.000
Standard error	0.017	0.027	0.028	0.017
EST-2				
Estimate	**0.058**	**0.089**	−0.062	−0.027
Normalized[b]	0.493	0.544	−0.316	−0.376
Standard error	0.019	0.027	0.028	0.020

[a] Estimates in boldface are highly significant ($P \ll .01$), whereas those underlined are significant at $P < .05$ [statistical test procedures from Asmussen and Basten (1994)].

[b] Relative to the maximum disequilibrium possible with the observed sign (Asmussen and Basten 1996).

Table 3. Cytonuclear genotypic counts for the 67 specimens of black bass with nonparental (i.e., hybrid) multilocus genotypes sampled from Lake Chatuge

mtDNA	AA	AB	BB	Total
Malate dehydrogenase-B (*sMDH-B*)				
M	20	25	1	46
	(15.8)	(27.4)	(2.7)	
m	3	15	3	21
	(7.2)	(12.5)	(1.3)	
Total	23	40	4	67
Phosphoglucomutase-A (*PGM-A*)				
M	31	15	0	46
	(24.7)	(19.2)	(2.1)	
m	5	13	3	21
	(11.2)	(8.8)	(0.9)	
Total	36	28	3	67
Esterase-2 (*EST-2*)				
M	30	13	3	46
	(24.0)	(17.2)	(4.8)	
m	5	12	4	21
	(10.9)	(7.8)	(2.2)	
Total	35	25	7	67

At each nuclear locus, A and B refer to marker alleles from spotted bass and smallmouth bass, respectively. For mtDNA, the respective haplotypes from these two species are denoted M and m. In parentheses are expected counts for the cytonuclear genotypes calculated from the marginal frequencies, assuming random associations.

"smallmouth-bass" allele at *sMDH-B* in spotted bass from Carters Lake; $2N$ = 74 (Pierce 1995)]. The second caveat is potentially more important. With only three diagnostic nuclear markers available, the probabilities of misclassification of an individual are nontrivial, but can also be specified precisely in some cases [by procedures detailed in Lamb and Avise (1987)]. For example, under the rules of Mendelian inheritance for three independent nuclear loci displaying fixed allelic differences, a true first-generation backcross individual might be mistaken as an F_1 hybrid with probability $(0.5)^3 = 0.125$, or alternatively (and with the same probability) as a pure member of the parental species to which it was backcrossed.

A substantial fraction of individuals (27.2%) in the Lake Chatuge collection displayed cytonuclear genotypes other than those expected in pure spotted or smallmouth bass (Table 4). (This inference is essentially unaffected, however, by the annexation of mtDNA data to the allozyme information—only one additional specimen of presumed hybrid ancestry was identified, carrying mtDNA of smallmouth bass origin but being homozygous for spotted bass alleles at all three nuclear loci.) Most (95.5%, 21 of 22) of the smallmouth bass mtDNA haplotypes in the Lake Chatuge sample were present in hybrids, rather than in pure smallmouth bass. A nearly identical proportion of smallmouth bass nuclear alleles, 96.0% (121 of 126), was also carried by individuals of hybrid ancestry.

The distributions of mtDNA haplotypes among the allozymically inferred hybrid classes suggest effects of gender-based asymmetries in the hybridization process. Six of the seven presumed F_1 hybrids (85.7%) displayed smallmouth-type mtDNA (Table 4), a finding that contributes to the disproportionate representation of smallmouth mtDNA among the single-locus nuclear heterozygotes (described above). All four individuals representing presumptive backcross hybrids to smallmouth bass displayed smallmouth bass mtDNA, as might be expected given the mtDNA composition of the F_1 hybrids (because all male and most female F_1s that backcross to smallmouth bass would produce offspring with smallmouth-type mtDNA). Among the individuals representing backcross hybrids to spotted bass, mtDNA haplotypes from both parental species were reasonably well represented (but see Discussion), as also might generally be expected (because most female F_1s backcrossing to spotted bass would produce backcross progeny with smallmouth mtDNA, whereas all reciprocal backcrosses to spotted bass would produce offspring carrying spotted bass mtDNA).

Discussion

Hubbs and Bailey (1940) appear to have been the first to identify natural hybrids between *Micropterus* species, but they concluded that hybridization in the genus was "extremely rare." Nonetheless, *Micropterus* hybrids can be produced in the laboratory (Wheat et al. 1971; Whitt et al. 1971), and several instances of introgressive hybridization in nature have been documented (Koppelman 1994; Whitmore and Hellier 1988), often following introductions of one bass species into the range of another (Morizot et al. 1991; Pierce 1995; Whitmore 1983). Here we have employed cytonuclear genetic markers to document the extent and gender-based pattern of introgressive hybridization following a transplantation of *M. punctulatus* into a reservoir containing native *M. dolomieui*.

Table 4. Counts of mtDNA haplotypes characteristic of spotted bass and smallmouth bass in various parental and hybrid classes of Lake Chatuge fish as provisionally identified by multilocus allozyme genotype (see text)

	Allozyme-based classification					
mtDNA	Spotted bass	Smallmouth bass	F_1	Backcrosses to spotted bass	Backcrosses to smallmouth bass	Other[a]
Spotted bass	178	0	1	41	0	4
Smallmouth	1	1	6	8	4	2

[a] F_2 or other later generation hybrids.

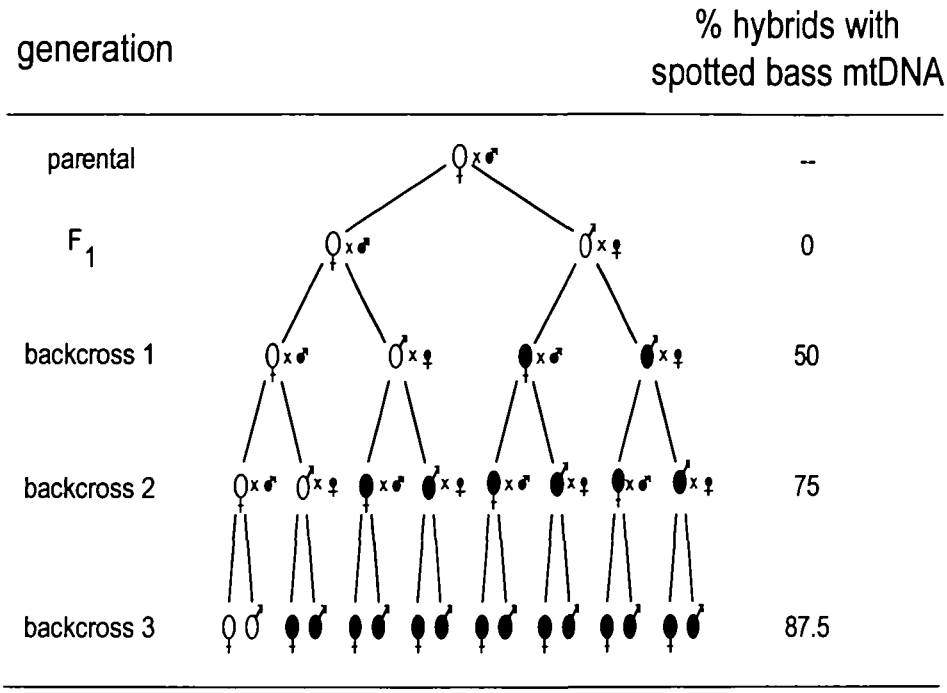

Figure 2. Diagrammatic representation of the increase in the population frequencies of spotted bass mtDNA haplotypes expected in successive generations of unidirectional backcrossing to spotted bass, assuming that all F_1s have smallmouth mothers and that hybrid fish of both genders participate equally in the formation of each backcross generation. Solid and open symbols indicate individuals carrying spotted bass and smallmouth bass mtDNA, respectively. After the parental generation, large gender symbols represent the fish of hybrid ancestry in the cross and smaller symbols always indicate pure spotted bass.

Introgressive Swamping and Faunal Turnover

The addition of mtDNA data to the allozyme information has furthered an understanding of the smallmouth/spotted bass population in Lake Chatuge. First, it adds to the genetic evidence for a profound faunal turnover following the introduction of nonnative spotted bass into Lake Chatuge some 10–15 years ago. The cytoplasmic markers are entirely consistent with those from the nucleus in documenting that the formerly abundant smallmouth bass population has declined dramatically over this period and been replaced by spotted bass and spotted/smallmouth hybrids, which together now account for more than 99% of the sampled specimens. The reasons for this species shift remain unknown, but the fact that the abrupt changes in absolute abundance of the two basses were temporally coincident [see census data for the period 1986–1989 in Pierce (1995)] suggests either that behavioral interactions between the two, and/or ecological or environmental changes that affected both simultaneously, may have been responsible. The precise nature of any such factors, however, remains entirely conjectural in the absence of detailed field studies of habitat requirements and ecological interactions between these species in Lake Chatuge.

Second, the mitochondrial data corroborate a scenario of introgressive swamping (or genetic assimilation; see Ellstrand 1992) of the native smallmouth bass population by introduced spotted bass. Based on our samples, about 95% of the remaining smallmouth bass mtDNA haplotypes (as well as nuclear alleles) in Lake Chatuge currently are housed in individuals of hybrid ancestry. These data do not imply that genetic assimilation was the primary cause of the decline in the smallmouth bass population in Lake Chatuge, but rather merely that the process has generally accompanied the shift in species abundances. Furthermore, it seems unlikely that introgressive swamping alone could account for the smallmouth decline, because the spotted bass was almost certainly the much rarer species in Lake Chatuge immediately following its introduction.

Third, the observed magnitudes and patterns of cytonuclear disequilibria document significant excesses of pure parental species genotypic classes (relative to random-association expectations from the marginal allelic frequencies in a contingency table). In the total data set (Table 1), such cytonuclear associations could in principle be promoted by continued migration of pure parental species into the lake, homospecific assortative mating, and/or selection against hybrids. The first explanation is unlikely, because Lake Chatuge is effectively a closed body of water to bass immigration (though it might be possible for smallmouth bass to migrate in from upstream reaches of the Hiawassee River). The possibility of selection against hybrids, although generally consistent with available genetic data, is difficult to critically evaluate against formal models because of the rapidly changing genetic composition of the Lake Chatuge population and its obvious nonequilibrium nature. Interestingly, however, these trends in multilocus association are also displayed by the class of individuals of hybrid ancestry (Table 3). Cruzan and Arnold (1993) interpreted such associations in a hybrid population of *Iris* plants as evidence for selection and assortative mating involving genotypes most similar to those of the pure parental species.

Finally, the cytonuclear data indicate a disproportionate representation of smallmouth bass mtDNA (and hence of smallmouth maternal lineages) in certain classes of Lake Chatuge hybrids. An inferred gender-based directionality to hybridization is evidenced most clearly by the predominance of smallmouth bass mtDNA in F_1 hybrids (six of seven individuals) and by the exclusive appearance of smallmouth mtDNA in our sample of backcross hybrids to smallmouth bass. However, among the progeny of inferred backcrosses to spotted bass, more than 80% (41 of 49 individuals) displayed spotted bass mtDNA, which may indicate the presence of later-generation backcross hybrids. As shown in Figure 2, the proportion of offspring carrying spotted bass mtDNA in this class of backcrosses should theoretically double in each successive backcross generation, provided that the reciprocal crosses with respect to gender are equally frequent. Thus, under this scenario, first-, second-, and third-generation backcross classes to spotted bass should display mtDNA in frequencies of about 50%, 75%, and 87.5%, respectively. Such backcross generations are likely in Lake Chatuge, given the age of the introduction and black bass generation lengths (about 2–5 years). In accounting for the high frequency of spotted bass mtDNA observed in these backcross hybrids in Lake Chatuge, it should be remembered that the probable inclusion of early generation backcross

hybrids in the collections might well be offset by the presence of later generation backcross progeny that would have been difficult to distinguish from pure spotted bass based on the three nuclear marker loci employed.

In cytonuclear genetic examinations of natural hybridization involving other species of Centrarchidae, Avise and Saunders (1984) noted a strong tendency for locally rare (as opposed to common) species to provide the female parent in interspecific crosses. This same pattern appears to hold at the present time for the spotted/smallmouth complex in Lake Chatuge, where spotted bass greatly predominate, yet most F_1s have smallmouth bass mothers. It is less clear, however, that this gender-based asymmetry of hybridization was always true in Lake Chatuge, because even if most F_1s historically had smallmouth bass mothers (as is tentatively suggested by the backcross data), this species did not become numerically rare until about 1989 (Pierce 1995).

In summary, although hybridization between smallmouth bass and spotted bass had been suspected by fishery biologists working in Lake Chatuge, neither the magnitude nor pattern of introgression could have been fully anticipated from casual morphological inspections alone. Thus, the cytonuclear examinations have added considerable detail to the description of genetic assimilation and species turnover in this reservoir.

Implications for Fisheries Management and Conservation

Following the arrival of a nonnative species, declines in native species' abundance through introgressive swamping, ecological competition, or both are general sources of concern in conservation biology. Several cases have been documented in which native taxa appear threatened by introgressive hybridization in addition to ecological competition from human-introduced or otherwise range-expanded congeners (e.g., Allendorf and Waples 1996; Brochmann 1984; Cade 1983; Echelle and Connor 1989; Ellstrand 1992; Rieseberg and Swensen 1996; Wayne 1996; Woodruff and Gould 1987). Because of concerns about extinction at the species level, most such case studies have monitored responses in rare or localized endemics to foreign introductions.

The black basses of Lake Chatuge provide another example in which the introduction of a nonnative species has been followed by a severe decline in abundance of a native congener and extensive introgressive hybridization. However, both spotted bass and smallmouth bass remain abundant elsewhere, are geographically widespread, and have allopatric strongholds in coastal drainages of the southeastern United States and in the Great Lakes region, respectively. Thus any immediate conservation concerns for the basses arising from the current analysis are primarily local rather than species threatening. Fisheries biologists and their constituents must decide whether the replacement of smallmouth bass by spotted bass and hybrids in Lake Chatuge has been desirable or injurious to the sport fishery (see Addendum). Rather, the broader significance of this study lies in the object lesson it provides with regard to human-mediated introductions, which the data demonstrate can have rapid, dramatic, and sometimes unanticipated genetic and demographic consequences for the species involved.

Addendum

In January 1995, an inquiry was made to the North Carolina Wildlife Resources Commission concerning a possible state record "spotted bass" that had been caught in Lake Chatuge in December 1994. The bass weighed 8 pounds, 14 ounces, and would have eclipsed the prior state record for that species by almost 3 pounds. However, visual inspection of the fish showed it to be intermediate in coloration and meristic characters between spotted and smallmouth bass (Clemmons M, personal communication). Tissues subsequently sent to our laboratory for molecular genetic examination revealed the specimen to be heterozygous at all three species-diagnostic allozyme loci employed in the current study and to possess spotted bass mtDNA. Thus the individual was most likely an F_1 hybrid between a spotted bass female and smallmouth bass male. On the basis of this combined morphologic and genetic evidence, official certification was denied this specimen as a state record for spotted bass.

Interestingly, the prior three North Carolina state records for "spotted bass," posted in 1991, 1992, and 1992, respectively, all came from Lake Chatuge (and all from the Shooting Creek arm of the lake). None of these fish has been examined genetically.

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